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Threats at home? Assessing the potential ecological impacts and risks of commonly traded pet fishes

James W. E. Dickey[1,2,3,4,5], Gareth Arnott[5], Ciara L. O. McGlade[5], Andrew Moore[5], Gillian E. Riddell[5], Jaimie T. A. Dick[5]

1 *Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany* **2** *Freie Universität Berlin, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany* **3** *Berlin-Brandenburg Institute of Advanced Biodiversity Research, Königin-Luise-Str. 2-4, 14195 Berlin, Germany* **4** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany* **5** *Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, Northern Ireland BT9 5DL, UK*

Corresponding author: James W. E. Dickey (jdickey03@qub.ac.uk)

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Abstract

Invasive alien species (IAS) are major drivers of global biodiversity loss, and the poorly regulated international pet trade is a source of emerging and future invaders. Predictions of the likely ecological impacts and risks of such IAS have been significantly enhanced in recent years with new metrics, which require application to many more actual and potential IAS. Hence, this study assesses the potential ecological impacts and risks of two readily available pet trade species: goldfish, *Carassius auratus*, a species with non-native populations worldwide; and white cloud mountain minnow, *Tanichthys albonubes*, a species with a limited invasion history to date. First, we compared the *per capita* feeding rates of these non-native species with two European trophically analogous natives – the stone loach, *Barbatula barbatula*, and the common minnow, *Phoxinus phoxinus* – using the Comparative Functional Response method. Second, we used foraging experiments in conspecific pairs to determine synergistic, neutral or antagonistic intraspecific interactions. Third, we performed novel object experiments using the two pet trade species to assess boldness, a known "dispersal enhancing trait". Goldfish had the highest maximum feeding rates of the four species, while white cloud mountain minnows had the lowest. Neutral interactions were observed for all four species in the paired foraging experiments, with goldfish having the highest consumption and white cloud mountain minnows having the lowest. Goldfish demonstrated greater boldness, being more active during the experimental trials and more likely to approach a novel object than white cloud mountain minnows. Further, combining maximum feeding rates, boldness and species availabilities from our survey of pet shops, we assessed the relative invasion risks (RIR) of the two non-natives. This highlighted goldfish as

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the higher risk and most worthy of management prioritisation, mirroring its more extensive invasion history. We propose that such metrics have potential to direct future IAS policy decisions and management towards the ever-increasing rates of biological invasions worldwide.

Keywords
Behaviour, functional response, invasive alien species, pet trade, propagule pressure, relative invasion risk

Introduction

The global spread of invasive alien species (IAS) is a major driver of biodiversity loss (IPBES 2019), and can lead to severe ecological, economic, social and health implications (Laverty et al. 2015; Cuthbert et al. 2021; Diagne et al. 2021). Increasing globalisation has facilitated new pathways for IAS to spread (Hulme 2009; Zieritz et al. 2016), with the number unlikely to saturate in the future (Seebens et al. 2018, 2021). One industry that has benefited from increasing globalisation has been the pet trade. Known to be poorly regulated (Raghavan et al. 2013), and with associated laws often poorly communicated and enforced (Patoka et al. 2018), it has facilitated the spread of a number of high-profile IAS around the world (Lockwood et al. 2019) and is deemed responsible for a third of all aquatic IAS (Padilla and Williams 2004).

While most species in the pet trade spend their entire lives in confinement, many are released or escape from producers, importers, retailers and owners, and can exert impacts on recipient ecosystems through predation, competition with natives, hybridisation, habitat degradation and the spread of disease and associated biota (Polo-Cavia et al. 2010; Kraus 2015; Mrugała et al. 2015; Emıroğlu et al. 2016; Patoka et al. 2016, 2020; Lozek et al. 2021). Reasons for release include displays of aggression, increasing size, and maintenance costs (Duggan et al. 2006; Fujisaki et al. 2010; García-Díaz et al. 2015), or high reproductive output leading to overstocked tanks (e.g. marbled crayfish, *Procambarus virginalis*: Chucholl et al. 2012). Furthermore, prayer release, the Buddhist and Taoist practice in which the liberation of animals is thought to improve karma, is an overlooked introduction pathway that often involves releasing animals acquired from pet stores (Liu et al. 2012; Magellan 2019; Wasserman et al. 2019; Marková et al. 2020). The likelihood of IAS establishment is heavily dependent on propagule pressure (the number, frequency and viability of individuals of each species released), and in the context of species in the pet trade, likelihood of escape or release depends on species availability (Duggan et al. 2006; Chucholl 2013).

Two commonly traded species are goldfish, *Carassius auratus*, and white cloud mountain minnows, *Tanichthys albonubes*. The former is deemed one of the world's worst invasive species (Beatty et al. 2017), and has established populations around the world (Lorenzoni et al. 2018) in both lotic and lentic habitats (Kim et al. 2014). Indigenous to East Asia, it is one of the world's oldest domesticated fishes (Balon 2004; Novák et al. 2020). Known to be tolerant of a wide range of abiotic conditions, goldfish have been implicated in the spread of parasites (Mouton et al. 2001), the decline

of native fishes (Deacon et al. 1964) and heavy grazing on aquatic plants (Richardson et al. 1995). Their method of benthic foraging is known to increase the turbidity of their habitats which in turn can affect competition with other species (Richardson et al. 1995), exacerbate algal blooms (Morgan and Beatty 2007), make them less visible to predators, and even allow them to regulate water temperature (Richardson et al. 1995). White cloud mountain minnows are endemic to southern China, and despite widespread popularity in the ornamental fish trade, they have a limited native distribution. Due to large-scale urbanisation and overexploitation by ornamental fishkeepers, they have been listed as a Class II protected animal in China's State Key Protected Animal List (Chan and Chen 2009). To date, there are a limited number of non-native populations – Colombia, Madagascar and Australia – but despite this and their global availability, little is known about their ecological impacts, actual or potential (Corfield et al. 2008). Our choice of these study species was informed by a 2017 survey of temperate/cold water species across twenty pet shops in Northern Ireland. With abiotic conditions such as temperature currently acting as a barrier to certain species in the pet trade from establishing and reproducing (Kalous et al. 2015; Standfuss et al. 2016), we highlighted which of the species recorded are capable of surviving temperatures of 10 °C or below. Of these, goldfish and white cloud mountain minnows were the most readily available (19/20 stores and 16/20 stores respectively: Suppl. material 1: Table S1).

Predicting ecological impacts and risks of such species was until recently deemed near-impossible (see Dick et al. 2014), with heavy reliance on invasion history, which is of little value prior to a species invading. However, new metrics combining traits and behaviour of species with easily measureable population metrics have enhanced impact and risk prediction (Dick et al. 2017b; Cuthbert et al. 2019b; Dickey et al. 2020). For example, the comparative functional response method, i.e. how consumption varies with resource availability for IAS relative to trophically analogous natives, has been highlighted as an effective way of assessing and predicting the ecological impacts of established, emerging and potential future non-native species (Dick et al. 2014).

One potential limitation of the comparative functional response method in measuring *per capita* consumption from the behaviour of individuals in isolation is that this misses the crucial role of intraspecific interactions inherent in group foraging, something particularly critical for assessing shoaling fish species. There are three broad categories of intraspecific interactions: neutral, antagonistic (prey risk reducing: Livernois et al. 2019), and synergistic (prey risk enhancing: Livernois et al. 2019), and accounting for this in the context of pet species releases, when small numbers of species might be released together, could prove valuable. There have also been calls for greater focus on behaviour in the study of invasive species, and specifically how the behaviour of successful IAS compare to less successful invaders (Rehage and Sih 2004). A number of behavioural traits have been deemed 'dispersal enhancing' (Rehage et al. 2016; Gruber et al. 2018). For example, boldness, i.e. how individuals behave in potentially risky situations (Réale et al. 2007), has been suggested to be a determinant of whether individuals are likely to disperse or remain sedentary, or whether they are short or long-distance dispersers (Fraser et al. 2001). How an individual, or group (see Kareklas et al.

2018), interacts with novel objects or shelter are commonly used methods of scoring boldness-like behaviour (Johnsson and Näslund 2018; McGlade et al. 2022).

Here, we thus sought to forecast the potential ecological impacts of goldfish and white cloud mountain minnows using three experiments: a comparative functional response study, an intraspecific paired feeding study, and a single and group boldness study; and then by combining this information into an adapted version of the Relative Invasion Risk (RIR) metric (Dickey et al. 2018). This three-pronged measure based upon the RIP metric (Dick et al. 2017b; Dickey et al. 2020) incorporates propagule pressure to assess the risk of a species establishing and exerting impact. We therefore used recent and new advances in IAS prediction metrics to assess the potential ecological impacts and risks of two non-native ornamental fishes, and discussed the general utility of these methods across the global pet trade.

Methods

Collection and husbandry

Goldfish were purchased from Carrick Pet Shop, Carrickfergus, Northern Ireland, over four batches due to availability (see Table 1 for further details). White cloud mountain minnows were purchased from Grosvenor Tropicals, Lisburn, Northern Ireland across two batches. For native comparators in the present study, we used two trophically analogous species (i.e. similar trophic ecology to the respective non-natives) commonly found in European temperate freshwater habitats. Firstly, we used the stone loach (*Barbatula barbatula*) as an example of a non-shoaling, benthic forager, more directly comparable to goldfish. Secondly, we used the common minnow (*Phoxinus phoxinus*), a species with a strong shoaling tendency (Magurran and Pitcher 1983) as a native analogue for the white cloud mountain minnow. Stone loaches were caught from the Minnowburn River by electrofishing on 6 August and transported to Queen's University Belfast School of Biological Sciences in a large barrel of continually aerated source water. Minnows were caught by hand net from Six Mile Water River on the 14 June 2019, and like the stone loaches, transported to the lab in aerated source water. All fish were maintained in glass holding aquaria (39.5 × 25 × 27 cm) within a controlled temperature laboratory with a temperature of 13 °C (+/- 1 °C) and a 12:12 light schedule, with experimental trials taking place in the same laboratory. Fish were given at least five days of adaptation to lab conditions before trials began. Holding aquaria contained an air stone, a filter and stones, plastic pipes and artificial plants to provide habitat enrichment. All fish were maintained on a diet of defrosted *Artemia* spp. (Monkfield Nutrition) and fed *ad lib* in the morning and the evening daily. To minimise disturbance to the fish, half water changes (as opposed to full water changes which require the potentially stressful removal of the fish) were performed weekly. Animal care was in accordance with institutional guidelines.

Table 1. Standard length and collection information for the four study species.

Study species	Standard length, mean ± SE	Origin	Collection date
Goldfish	49.6 mm +/- 0.76	Carrick Pet Shop, Carrickfergus	Batch 1: 16 July 2019, n = 8; Batch 2: 27 July, n = 12; Batch 3: 8 August, n = 12; Batch 4: 30 August, n = 8
White cloud mountain minnow	24.9 mm +/- 0.34	Grosvenor Tropicals, Lisburn	Batch 1: 5 July 2019, n = 20; Batch 2: 24 July, n = 20
Stone loach	61.4 mm +/- 0.90	Minnowburn River (54°32'54.7"N, 5°57'09.4"W)	6 August 2019
Minnow	41.2 mm ± 0.05	Six Mile Water River 54°42'16.6"N, 6°12'14.9"W	14 June 2019

Functional response

Fish were starved for 24 hours before functional response experiments began. Live bloodworm prey (*Chironomus* spp.), which all species were observed to readily consume, was offered as an ecologically relevant species in densities of 2, 4, 8, 16 and 32 (n = 3 per prey density, per species). Trials took place in acrylic tanks (22 cm × 17 cm × 22 cm) filled with 2 L of dechlorinated tap water that had been oxygenated overnight, and covered in masking tape so as to prevent any external visual disturbance. Trials ran for two hours, after which time the remaining alive prey were counted. Due to the high consumption rates of goldfish, additional prey densities (64 and 120) were offered to find a density that eventually led to the consumption rate reaching an asymptote for this species.

Paired feeding

Fish were starved for 24 hours prior to trials commencing. Trials took place in masking taped 10-L plastic aquaria (31.5 cm × 16.6 cm × 18.6 cm) filled with 6 L of dechlorinated tap water. Fish densities of 1× and 2× were used, with a constant density of bloodworm prey offered. This prey density was to be 60 bloodworms across all species, but this was increased to 240 for goldfish after pilots revealed their higher prey consumption rates relative to the other study species. To prevent any confounds ensuing from greater oxygen consumption in paired versus individual treatments, each arena was aerated via a portable, battery powered pump. Trials ran for 2 hours, after which time the number of live prey was counted.

Novel object test for goldfish and white cloud mountain minnows

This experiment occurred in batches of four fish individuals (6 batches, n = 24 individuals per species). Fish were selected from the holding tank and added individually to one of four masking taped plastic arenas (31.5 cm × 16.6 cm × 18.6 cm) containing 4 L of dechlorinated tap water, with four equally sized zones marked on the base, and a metal mesh placed over the first zone (Zone 1) to offer shelter (see Suppl.

material 2: Fig. S1). To avoid any effects of differing hunger levels (e.g. Nakayama et al. 2012), fish were given 10 defrosted *Artemia* spp. during a 30-minute adaptation period in their arenas (see Suppl. material 3: Fig. S2 for experimental procedure timeline), with an air stone added and green plastic sheets placed over the top. A 5-minute buffering period began with the commencement of recording using a camera (CX Action Camera, ACTIVEON Inc., U.S.A.) held above the arena with a retort stand, and removal of the air stone and the cover. Fish were exposed to two treatments, a "trial" (in the presence of the object) and a "control" (in the absence of the object) treatment to compare behaviour in the presence of the object with behaviour in an empty arena. Both treatments were 10 minutes long with their order randomised and balanced, so that half were trial then control, and half were control then trial (see Suppl. material 3: Fig. S2). This was done to prevent temporal confounds, such as the effect of familiarity with the arena or the effect of oxygen level on behaviour. Trial treatments were initiated by the dropping of the novel object (a blue plastic air stone splitter attached to string) into Zone 4, with the arenas subsequently recorded for another 10 minutes. Control treatments, in the absence of the novel object, commenced upon the removal of the novel object (when the order was trial-control) or the ten minutes prior to the addition of the novel object (when the order was control-trial). The string attached to the novel object was used to add and retrieve it in a way that minimised disturbance to the fish, as well as to ensure the novel object was confined to Zone 4 throughout. Once complete, all four fish were weighed, measured, and recorded being added into a fifth arena one at a time in advance of the group trial commencing. Again, a five-minute period took place before another paired trial/control treatment (order of treatments consistent with previous experiment) using a different novel object of differing shape and colour to maintain novelty – a small, grey, plastic koala figure again attached to string to enable retrieval (Suppl. material 3: Fig. S2). Behavioural analysis was conducted from video footage using BORIS v7.4.14 (Friard and Gamba 2016). For both individual trials and controls, the time spent in each zone was recorded, as was the summed total number of occurrences in each zone, which was used as a proxy for fish activity. For individual trials, the latency to approach the novel object, the number of approaches and the number of trials in which an approach was made was recorded, with an approach defined as contact between the fish and the object. In group trials, the latency was recorded as the time taken for the first fish individual to approach the novel object.

Data analyses

Functional response

Functional Responses (FR) were modelled using the 'frair' package (Pritchard et al. 2017).

Logistic regression of the proportion of prey consumed as a function of prey density was used to infer functional response types (Juliano, 2001). Here, a significantly negative first-order term is indicative of a Type II FR, whilst a significantly positive

first-order term, followed by a significantly negative second-order term, is considered a Type III FR. As prey were not replaced as they were consumed, Rogers' random predator equation was used to model FRs (Rogers, 1972):

$$N_e = N_0 (1–\exp(a(N_e h–T))) \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental period. Maximum feeding rates ($1/h$) were calculated under each treatment group. The *Lambert W* function was used to solve the random-predator equation (Bolker 2008). Non-parametric bootstraps (n = 2000) were used to generate 95% confidence intervals around FR curves, which were assessed visually for overlap.

Paired feeding

Per capita consumption was analysed via linear modelling with respect to species and predator density. Non-significant terms were removed stepwise (Crawley 2013), and Tukey's HSD post-hoc testing was performed using the lsmeans package (Lenth 2016).

Novel object

The number of individuals that approached the novel object was compared between species using Pearson's Chi-squared test, with Yates' continuity correction. Generalised linear modelling (Quasipoisson family) was used to assess the effect of species on the numbers of approaches and the individual and group latencies to approach. The latency to approach for groups was measured as the time taken for the fastest fish in the group to approach, which was compared with the time taken by the fastest of the four fish making up the batch in the individual tests (i.e. individual/group a variable in the model). For all models, backward reductions of non-significant terms and interactions facilitated the most parsimonious fits (Crawley 2013). The number of occurrences in each zone (which unlike approach measures occurred under both trial and control experiment treatments) was analysed with respect to species and experiment treatment (i.e. trial or control) with a generalised linear mixed model (Poisson family), with arena number (see Suppl. material 2: Fig. S1) as a random factor. Due to overdispersion, observation level random effects were used (Harrison 2014). The effect of experimental treatment (i.e. trial or control) and species on the time spent in the sheltered Zone 1 (time spent in other zones not analysed) was assessed using a linear mixed model with arena number as a random factor. Generalised linear models showed no significant effect of trial order (trial-control versus control-trial) on all the recorded measures.

Relative invasion risk

Dickey et al. (2018) defined invasion risk as the product of maximum feeding rate (derived from Functional Response experiments), a relevant life history trait as a proxy

for the numerical response (e.g. lifespan, fecundity or lifetime fecundity), and pet propagule pressure (the proportional availability of the species from the pet stores surveyed). Relevant life history traits are often unavailable for pet species or based entirely upon observations in captivity. The adapted versions of the Invasion Risk (IR) metric used here are thus based upon maximum feeding rates taken from the functional response experiments, likelihood of approaching the novel object taken from the behaviour experiment as a life history trait alternative, and propagule pressure taken from a survey of temperate, freshwater fishes across twenty Northern Irish pet shops between the 31 January and 1 March 2017 (Suppl. material 1: Table S1). Firstly, we put forward a measure of IR that accounts for behaviour (IR_b):

$$IR_b = FR \times Boldness \times PPP \quad (2)$$

This is most similar to the version of IR featuring in Dickey et al. (2018). However, that study compared four trophically similar turtles and assessed their risk of establishing relative to each other in an ecosystem lacking native analogues. Here, one could argue that the study species are more trophically similar to the native species used rather than each other, with goldfish and stone loach two benthic foragers, and white cloud mountain minnows a shoaling species similar to common minnows. For that reason, a measure of risk should account for their impacts relative to the most trophically analogous natives, rather than each other. We therefore introduce a second IR measure that accounts for behaviour and trophic level, IR_{bT}. This incorporates a measure of relative maximum feeding rate (FR_r) of each pet trade species (FR_{inv}), taking account of the feeding rates of the closest native trophic analogues (FR_{nat}):

$$FR_r = \frac{FR_{inv}}{FR_{nat}} \quad (3)$$

Using this measure can allow multiple pet trade species from different taxonomic groups, with different ecological roles, and hence different trophic analogues, to be visually compared and prioritised, provided the measure of boldness (or other trait) is relevant for all. We can therefore define our second measure of IR (IR_{bT}) as:

$$IR_{bT} = FR_r \times Boldness \times PPP \quad (4)$$

As in Dickey et al. (2018), these three-pronged risk assessment metrics can be displayed visually using three dimensional graphs, with invasion risk increasing towards the top right corner. Alternatively, the Relative Invasion Risk score can be calculated for both measures:

$$RIR_b = \frac{IR_{\text{b.inv 1}}}{IR_{\text{b.inv 2}}} \quad (5)$$

$$RIR_{bT} = \frac{IR_{bT \cdot inv1}}{IR_{bT \cdot inv2}} \quad (6)$$

Like the RIP score as proposed by Dick et al. (2017b), when the resulting RIR value is < 1, this predicts "invader 1" will be lower risk than "invader 2"; when RIP = 1, we can predict the risk of "invader 1" to be no different from that of "invader 2"; and when RIP is > 1, we can predict that "invader 1" will be higher risk than "invader 2".

All statistical analyses were carried out in R v.3.2.2 (R Core Development Team 2015). Scripts for functional response analysis and Relative Invasion Risk analysis available in the supplementary material of Pritchard et al. (2017) and Dickey et al. (2018) respectively.

Results

Functional Response

Prey survival in all control groups was 100%, and thus all prey mortality in experimental groups was attributed to fish predation, which was also directly observed. Type II functional responses were exhibited by all four species, as determined by significant negative first order terms (Table 2; Fig. 1). Goldfish had only the third highest attack rate but the shortest handling time, and hence a much higher maximum feeding rate than any of the other study species. White cloud mountain minnows exhibited the lowest attack rates and the longest handling times (and therefore the lowest maximum feeding rates, $1/h$, of the four study species). Stone loach had the second highest attack rate, and the second shortest handling time, and hence second highest maximum feeding rate after goldfish. Minnows had the highest attack rate, but the second longest handling time, after white cloud mountain minnows (Table 2; Fig. 1).

Paired feeding

Assessing the species given a fixed prey density of 60 (i.e. excl. goldfish), there was a significant effect of species on *per capita* consumption (linear model, LM: adjusted $R^2 = 0.68$, $F_{3,26} = 18.39$, $p < 0.001$; Fig. 2), with white cloud mountain minnows eating significantly less than stone loach ($p < 0.001$) and minnows ($p < 0.001$), and stone loach eating significantly more than minnows ($p = 0.002$). When goldfish (fixed prey density of 240) were included in the model (LM: adjusted $R^2 = 0.78$, $F_{4,35} = 31.85$, $p < 0.001$), their average *per capita* consumption rates were significantly higher than the others ($p < 0.001$ for all comparisons). Average *per capita* consumption was not significantly affected by predator density in either model (goldfish excluded: $p = 0.363$; goldfish included: $p = 0.302$).

Table 2. First order terms calculated from logistic regression to denote functional response type across all predator treatments. The significant negative first order term values across all four species indicate Type II functional responses for each predator. Attack rate (a), handling time (h) and maximum feeding rate (1/h) parameter estimates derived using Rogers' random predator equation (Eq. 1). '***' $p < 0.001$, '**' $p < 0.01$. '*' $p < 0.05$, '.' $p < 0.1$.

Species	Prey	First-order term	Attack rate (*a*)	Handling time (*h*)	Maximum feeding rate (1/*h*, prey per 2 hours)
Goldfish	Chironomid	-0.01**	2.26***	0.01***	217.64
White cloud mountain minnow	Chironomid	-0.09 ***	0.81.	0.35***	2.89
Stone loach	Chironomid	-0.06**	2.65***	0.02***	42.87
Common minnow	Chironomid	-0.11 ***	3.57**	0.09***	11.11

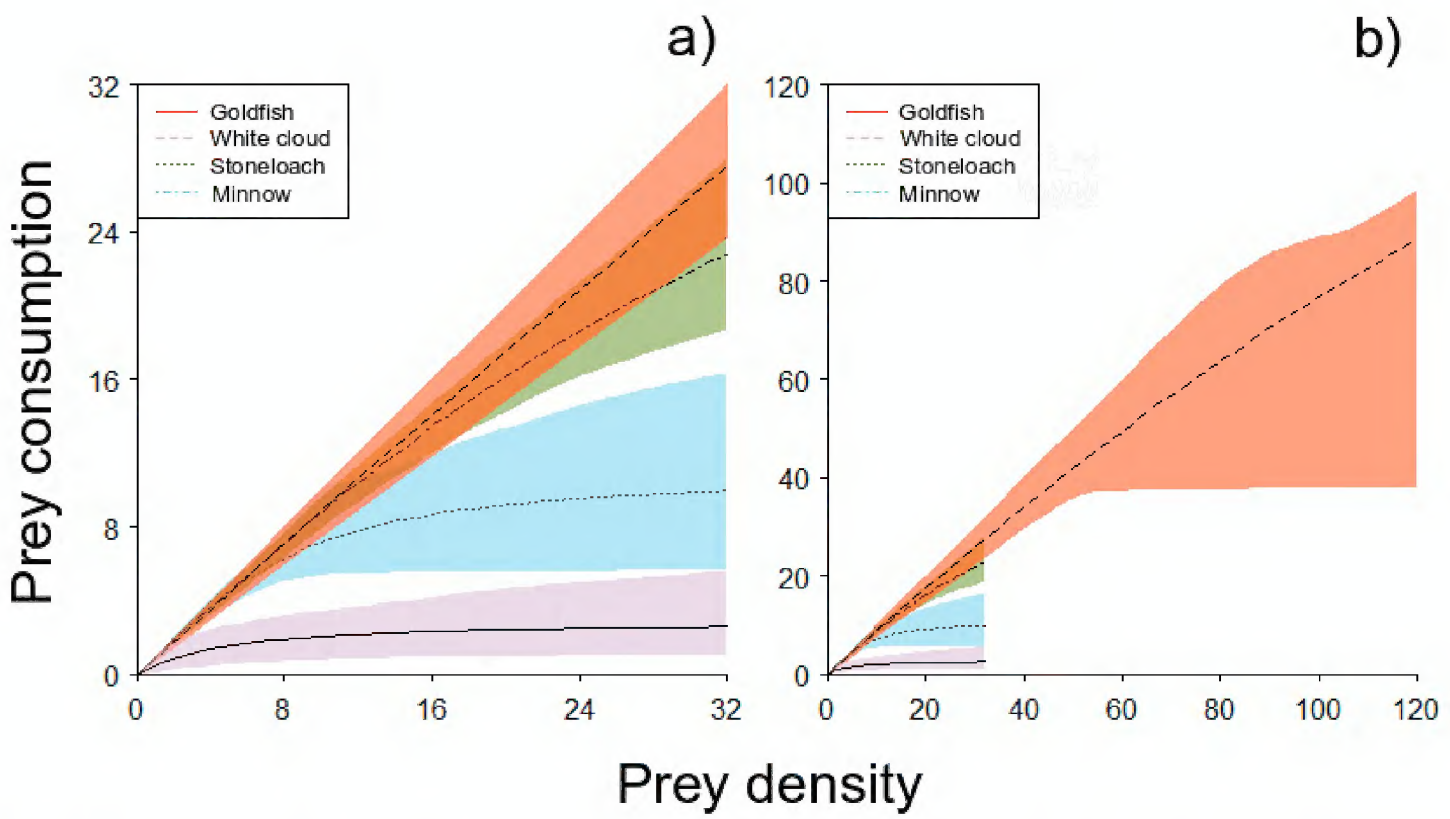

Figure 1. Functional response curves of goldfish, white cloud mountain minnow, stone loach and common minnow towards Chironomid prey. Shading represents 95% confidence intervals **a** all species compared over prey densities up to 32 **b** as per **a** but with prey dentities up to 120 to derive goldfish asymptote.

Novel object

Overall, goldfish were more likely to approach the novel object than white cloud mountain minnows (91.67% v 54.17% of trials out of 24 in which focal fish approached; $\chi^2 = 6.75$, df = 1, $p < 0.01$), however, of the individuals that did approach, the number of approaches did not differ by species. There was no significant effect of experimental order, i.e. trial-control versus control-trial, on the latency, number of approaches or activity (generalised linear models, GLM: $p = 0.255$, $p = 0.654$, $p = 0.795$). There were no significant effects of species or experiment type (i.e. single or group) on latency (GLM: $p = 0.571$, $p = 0.313$). Analysing activity levels, there were significant effects of species and

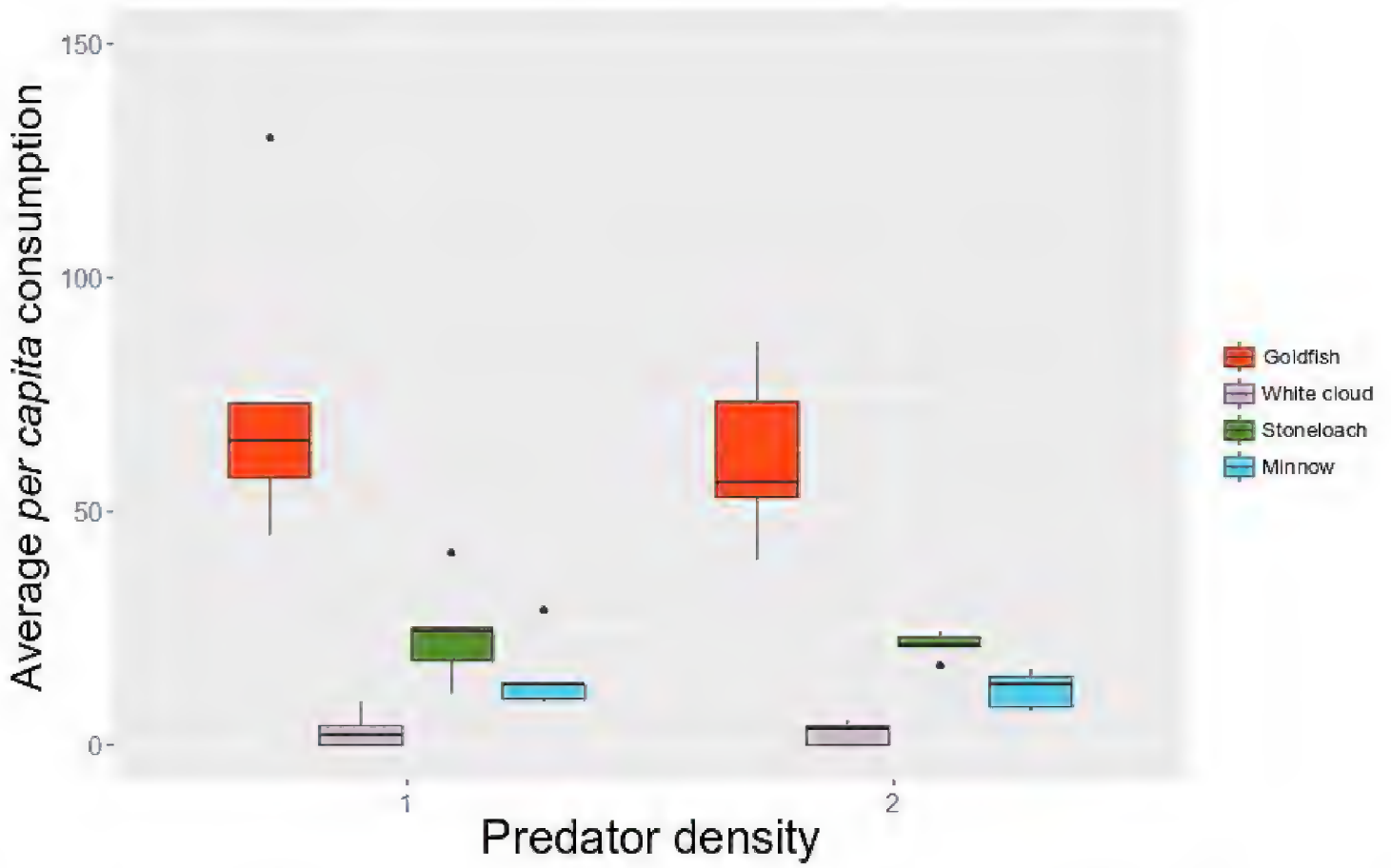

Figure 2. Average *per capita* consumption across single and pair predator densities in the group feeding trials. Fixed prey density of 60 bloodworms for white cloud mountain minnows, minnows and stone loach. Fixed prey density of 240 bloodworms for goldfish.

treatment type (i.e. trial v control), but no significant two-way interaction, with goldfish more active than white cloud mountain minnows ($z = 2.31$, $p = 0.02$: Fig. 3), and both species less active during trial experiments ($z = 2.03$, $p = 0.04$: Fig. 3). Assessing the effect of trial or control and species on the time spent in Zone 1 showed no significant finding.

Relative invasion risk

Using both RIR measures, goldfish were shown to have much higher invasion risks than white cloud mountain minnows, with both calculations giving scores > 1 (Table 3; Fig. 4). The RIR_b score was 151.56, with the difference in feeding rates the main driver of the large disparity (Table 3; Fig. 4a). Using RIR_{bT} however lessened this, giving a score of 39.29, due to a smaller relative maximum feeding rate of goldfish in relation to stone loach, the other benthic forager (Table 3; Fig 4b). Both scores highlight goldfish as a much greater invasion risk.

Discussion

In an increasingly globalised world, the need for methods to predict and prevent future IAS is vital (Diagne et al. 2021; Vilizzi et al. 2021). Here, we assessed two readily

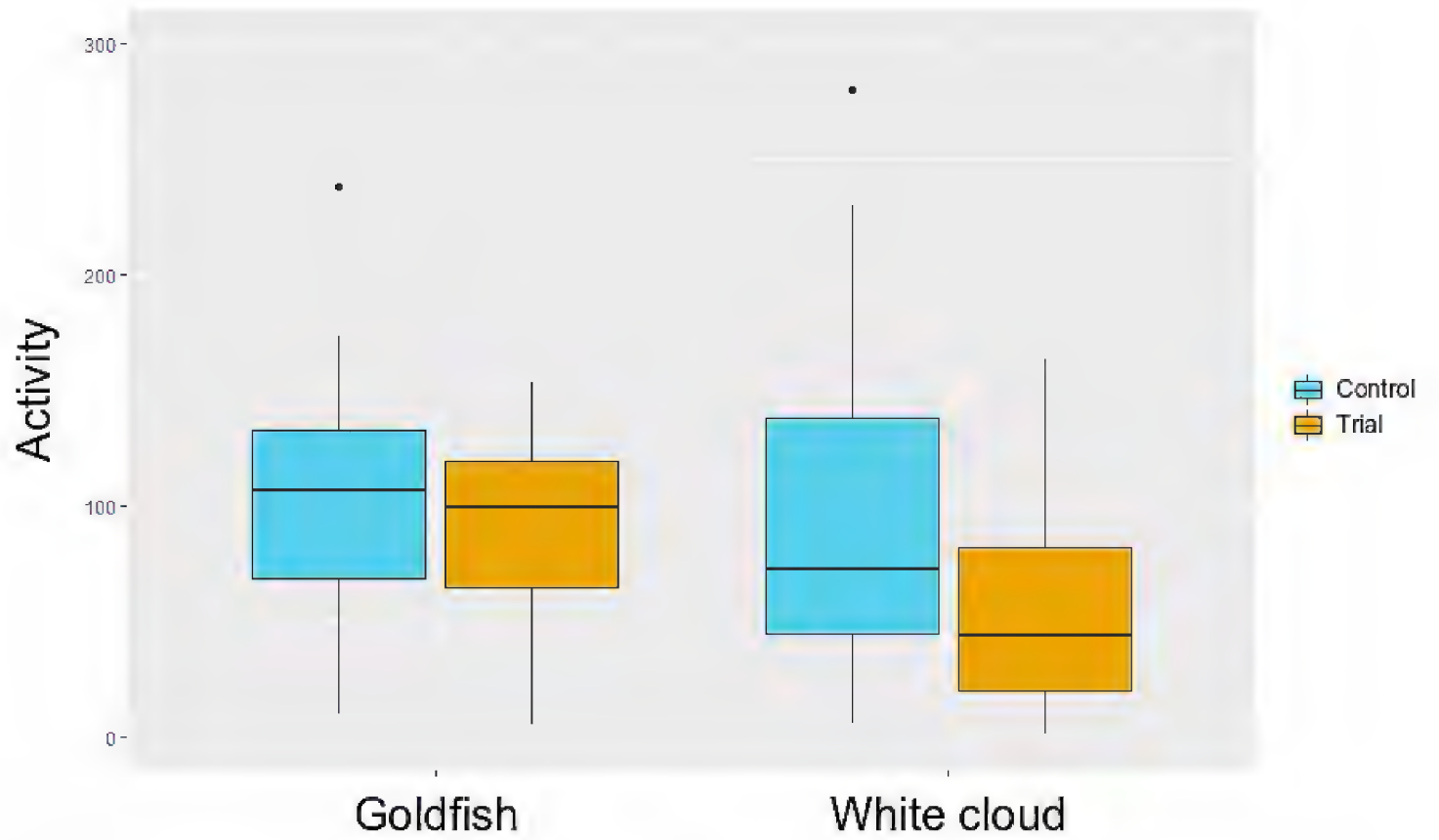

Figure 3. Goldfish and white cloud mountain minnow activity in control and experimental trials, as determined by the summed number of occurrences in each of the four zones.

Table 3. Relative Invasion Risk (RIR_b) and Trophic Relative Invasion Risk (RIR_{bT}) calculations, whereby RIR_b = maximum feeding rate (FR) × boldness (B) × pet propagule pressure (PPP), and RIR_{bT} = maximum feeding rate relative to trophically analogous native (FR_T) × boldness (B) × pet propagule pressure (PPP). The FR_{native} comparator for goldfish was the stone loach, and the native comparator for white cloud mountain minnow was the common minnow. The novel object approaches figure is the proportion of trials in which the species approached the novel object out of 24 trials. The Pet Propagule Pressure figure is the proportional availability of the species out of 20 surveyed pet shops (see Suppl. material 1: Table S1). IR_b is calculated as the product of FR, B and PPP. RIR_b is calculated by dividing the IR_b of goldfish by the IR_b of white cloud mountain minnow. IR_{bt} is calculated as the product of FR_T, B and PPP. RIR_{bT} is calculated by dividing the IR_{bT} of goldfish by that of the white cloud mountain minnow.

Species	FR	FR_{native}	FR_T	B	PPP	IR_b	RIR_b	IR_{bT}	RIR_{bT}
Goldfish	217.64	42.87	5.08	0.92	0.95	189.60	151.56	4.42	39.29
White cloud	2.89	11.11	0.26	0.54	0.80	1.25		0.11	

available species from the pet trade that are likely to be capable of surviving in a temperate zone: goldfish and white cloud mountain minnows. First, the comparative functional response (CFR) method compared these pet trade IAS with the trophically analogous native stone loach and common minnow. This method has proven robust in highlighting damaging invaders relative to trophically analogous native species or less damaging IAS based on their resource uptake rates (Bovy et al. 2014; Dick et al. 2014; Dodd et al. 2014). Second, we assessed the role that intraspecific group size plays on *per capita* foraging rates. Specifically, this was to reveal whether the presence of a conspecific led to intraspecific interactions that are neutral, i.e. average *per capita* feeding rates remained constant regardless of group size; synergistic, i.e. average *per capita* feed-

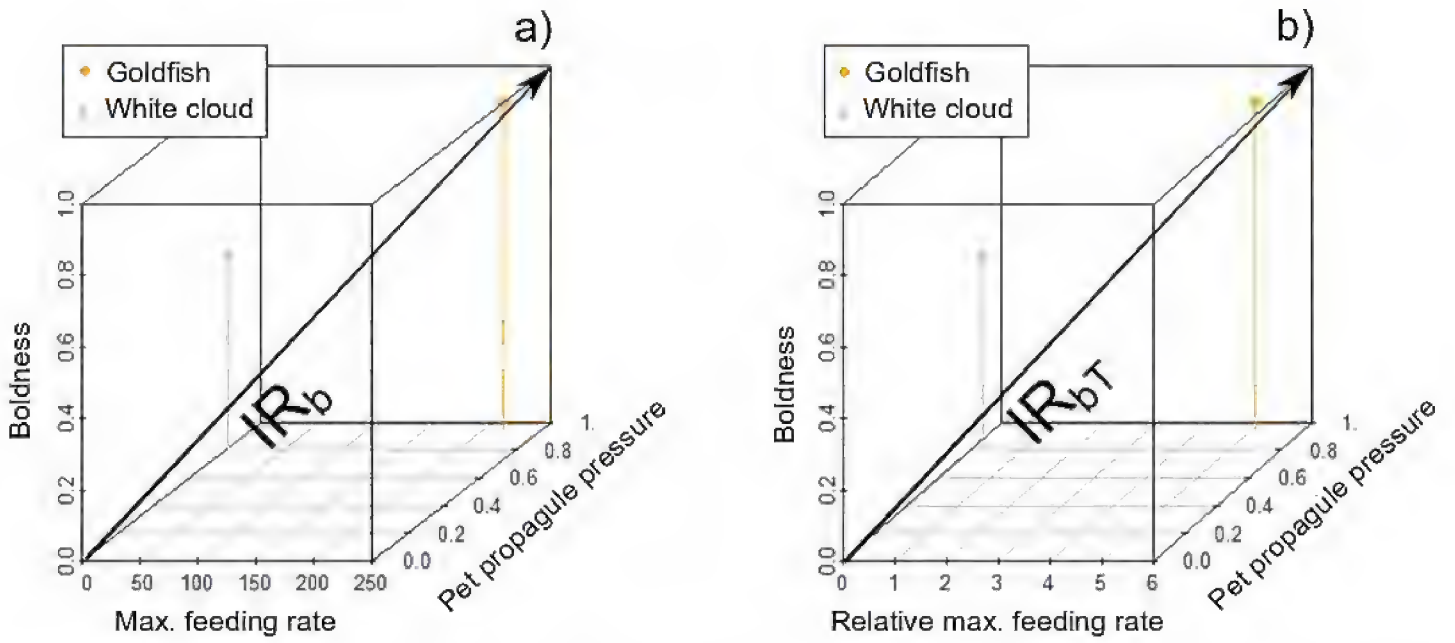

Figure 4. Three dimensional graphs showing Relative Invasion Risk (RIR) of goldfish and white cloud mountain minnows. RIR_b calculated as a product of maximum feeding rate, boldness, and Pet Propagule Pressure (PPP) **a** and RIR_{bT} calculated as the product of IAS maximum feeding rate divided by native analogue maximum feeding rate, boldness and PPP **b**. Invasion Risk increases from bottom left to top right of each plot.

ing rates increased in groups; or antagonistic i.e. group feeding reduced average *per capita* feeding rates (Livernois et al. 2019). Third, we compared goldfish and white cloud mountain minnow behaviour with and without the presence of a novel object in order to assess measures of boldness, a known "dispersal enhancing trait" (Gruber et al. 2018). Finally, this information was combined alongside availability measures from our pet store survey within two adapted versions of the Relative Invasion Risk (RIR) metric.

Functional response

All four study species exhibited potentially "destabilising" type II functional responses, however, there were clear differences in terms of attack rates, normally indicative of predation at low prey densities (Dick et al. 2014), and handling times and maximum feeding rates, used as an indicator of ecological impact (Dick et al. 2017a). Goldfish had only the third highest attack rate but the highest maximum feeding rate, indicative of a large ecological impact. With the study goldfish used having no known previous exposure to live prey, this suggests an adaptability to novel prey items, which has been demonstrated in prior experiments (Monello and Wight 2001). Despite being known to eat insect larvae in the wild throughout the year alongside zooplankton and detritus (Yi et al. 2004; Liang et al. 2008), white cloud mountain minnows had the lowest attack rates, and the lowest maximum feeding rates, suggesting a low ecological impact. Stone loach had the second highest attack rate and the second highest maximum feeding rate, while common minnows demonstrated the highest attack rate, but only the third highest maximum feeding rate. Chironomid larvae is known to feature in both native species' diets (Smyly 1955; Museth et al. 2010; Vinyoles et al. 2010), making similar percentage contributions (Frost 1943; Smyly 1955), and the differences here can likely be ascribed

to method of predation. Stone loach, with eyes located dorsally, tend not to rely on sight when foraging, instead using their barbels to sense prey (Smyly 1955), which may in turn have led to the minnow offering a greater predatory threat at low prey densities.

Paired feeding

This was done to address a shortcoming of recent impact assessment metrics (Dickey et al. 2020) which define impact as the product of the maximum feeding rate, as derived from functional response experiments, with a proxy of numerical response, normally species abundance or density. Such metrics have an inherent assumption that feeding rate increases linearly with predator numbers (i.e. neutral intrapecific interactions), and in turn fail to account for possible synergies or antagonisms between predators. The type of interaction may offer valuable insights into establishment and spread at different stages of the invasion process. For example, synergistic interactions, i.e. a lack of aggression towards conspecifics, have been thought to facilitate the success of the Argentine ant (*Linepithema humile*) in its introduced range (Suarez et al. 1999). Conspecific group foraging also confers numerous advantages in terms of finding and consuming food, and antipredator defence (Pitcher et al. 1982; Creel and Creel 1995), which may be of added importance in novel ecosystems.

Here, using our four study species across two different predator densities, a significant effect of species was found, but not for predator group size. In other words, we saw similar average individual feeding rates at both single and paired densities, and this was the case for all four species. The same pattern from the functional response experiment was shown, with goldfish having the highest consumption rates both singly and in pairs, with white cloud mountain minnows again having the lowest consumption rates. From this, we could therefore assign "neutral" rather than synergistic or agonistic interactions to all four species: a classification that here matches the inherent assumption of linearity of RIP. Neutral interactions for goldfish and stone loach were as expected as neither species is a shoaling species, with the former only truly social when breeding (Dunlop et al. 2006), and neither is known to be particularly aggressive towards conspecifics (unlike, for example, the benthic round goby, *Neogobius melanostomus*, Groen et al. 2012), with stone loaches typically found in small groups (Smyly 1955). However, the lack of effect of group size on foraging by the shoaling white cloud mountain minnows and common minnows was unexpected. It may suggest that the release of small numbers of white cloud mountain minnows would have neutral, and predictable additive effects. A study into the welfare implications of group size on white cloud mountain minnows (Saxby et al. 2010) showed no difference in the amount of "darting behaviour" – associated with predator avoidance, being chased or being unsettled – exhibited by groups of two fish relative to groups of 5 or 10. Similarly, there was no difference in time spent in an area of area of environmental enrichment relative to groups of 10, and fewer aggressive acts per individual than in groups of 5 and not significantly different to the number in groups of 10. However, groups of two still took significantly longer to start feeding relative to groups of 5 or 10, though significantly less than for individual fish, indicating decreased welfare from an unnaturally small

group size. Fish in small shoals are known to spend less time foraging than fish in larger shoals (Magurran and Pitcher 1983), and we therefore encourage future studies to investigate the effects of higher density treatments, especially for comparing the white cloud mountain minnow and common minnow.

Novel object

While invasion success depends on myriad factors and species traits, behaviour has been shown to play a major role (Weis 2010; Chapple et al. 2012), with a number of behavioural traits associated with invasion success and dispersal, such as boldness. One frequently used method to assess where individuals lie along the bold-shy axis and their degree of neophilia has been the novel object test, whereby satiated individuals are presented with an unfamiliar object, and the number of interactions are recorded per unit time. In novel object tests the approach is elicited by the object and not by any associated reward, as opposed to tests featuring novel food items for example (Kareklas et al. 2018), and therefore is a measure of attraction to intrinsically rewarding novelty (Griffin et al. 2016). This motivation to approach novel stimuli is deemed critical to persisting in new environments in which they lack specific knowledge for survival (Griffin et al. 2016). Here, we assessed boldness in the form of the likelihood of approaching the novel object, the latency to approach the novel object (both individually and in conspecific groups), the number of approaches, activity and the residency in the sheltered Zone 1 in the experimental arena. While a number of studies to date have compared measures of dispersal enhancing traits between non-native and native species, or invasion frontier versus long-established non-native populations (Rehage et al. 2016), we compared the two pet trade species: goldfish as a species with an extensive invasion history; and white cloud mountain minnows as one with a limited invasion history. In doing so, we found that goldfish were more likely to approach the novel object than white cloud mountain minnows, and were more active. Despite known tradeoffs associated with boldness (Stamps 2007), high boldness and activity levels have been shown to enhance feeding opportunities (Brownscombe and Fox 2013), survival in the presence of predators (Smith and Blumstein 2010; Blake et al. 2018), and boldness has also been shown to correlate to dispersal in the field (Fraser et al. 2001), as well as measures of reproductive success in other taxa (e.g. Collins et al. 2020). There was also a significant effect of trial/control on general activity levels, which may indicate a level of behavioural flexibility for both species, and context-specific adjustments of behaviour have been shown to be beneficial for a number of successful IAS (Sol et al. 2002; Cure et al. 2014). Of course, the degree of boldness demonstrated during the novel object test will have been determined by perception of costs by individuals of both species. While the specific drivers of the behaviour of both species are beyond the scope of this study, goldfish are larger than the white cloud mountain minnows, and greater size has been shown to facilitate greater risk taking, due to lower likelihood of predation (Ioannou et al. 2008). However, goldfish also have to balance this against colouration that makes them more visible to potential visual predators (their ability to change the turbidity of water bodies is deemed a survival benefit for this reason:

Richardson et al. 1995). It is important to note that black goldfish colour morphs exist and, conversely, gold colour morphs of *T. albonubes*. The degree to which colour affects behaviour and establishment success is a worthy avenue for further study. The mechanisms behind the costs and benefits perceived by individuals of both species are also shaped by evolutionary history in their native range (e.g. the nature of the predators of both species when in the wild), the number of generations of domestication (i.e. goldfish have been selectively bred for over 1000 years: Chen et al. 2020) and physiological drivers. Ultimately, these combine to give goldfish higher exploratory tendencies and, when combined with higher feeding rates, demonstrate what Rehage et al. (2016) describe as an 'invaders syndrome', which corroborates with them having established worldwide, being known to be highly motile in novel ecosystems (found to move up to 4 $km.day^{-1}$: Kim et al. 2014), and being expected to further expand their range in the near future (Beatty et al. 2017). Also, as a species regularly kept in outdoor ponds, they are at heightened risk of further spread (Copp et al. 2010; Patoka et al. 2017).

Relative Invasion Risk, implications and future studies

Our two measures of RIR allowed the key findings from the functional response and behaviour experiments to be combined alongside a measure of propagule pressure based on availability in the pet trade, to give an overall measure of invasion risk. Due to the lack of information available for our study species in the wild, we used a measure of boldness rather than life history traits (as used in Dickey et al. 2018), or alternative proxies of numerical response (Dickey et al. 2020). However, connections between boldness and reproductive fitness have been demonstrated. For example, bolder male zebrafish (*Danio rerio*) were shown to fertilise more eggs (Ariyomo and Watt 2012), boldness was associated with sperm number in male guppies, *Poecilia reticulata* (Gasparini et al. 2019), and moving beyond fish species, boldness and reproductive success are linked for black-legged kittiwakes, *Rissa tridactyla* (Collins et al. 2020). The two measures of RIR used in this study both demonstrated the greater risk posed by goldfish, albeit in subtly different ways. While RIR_b is closer in nature to the measure of RIR previously proposed (Dickey et al. 2018, 2020), it offers a risk assessment measure only focused on comparing the risks of the pet trade study species, that similarly allowed direct comparison between four pet trade turtles introduced into northern Europe with a lack of native analogues in Dickey et al. (2018). That is not the case here, and while a method of comparing two cyprinid fish species is valuable, their respective roles in a recipient ecosystem could prove very different. For that reason, a measure of RIR (such as our RIR_{bT}) that accounts for their feeding rates relative to trophically analogous native species, provides policy makers with a method that allows multiple pet trade species, across multiple taxonomic groups (e.g. fish, crayfish, shrimps), and at multiple trophic levels, to be compared and prioritised for risk, provided there are native analogues. Indeed, policymakers could decide upon a threshold IR_{bT} number, beyond which imports or sales of that species could be curtailed, dovetailing with or, for countries outside of the EU, offering an alternative to the list of Invasive Alien Species of Union Concern (Regulation 1143/2014).

It is important to note that functional responses, intraspecific interactions and behaviour of invasive species are not fixed, and they often change over the course of an invasion as the population is subjected to different selection pressures. This has been highlighted by a number of studies that have compared populations at the invasion frontier with long-established populations (Groen et al. 2012; Iacarella et al. 2015; Tarkan et al. 2021), populations in invaded ranges with those in the native range (Suarez et al. 1999; Howard et al. 2018), and in the context of pet species, those in captivity versus those that have established wild populations (Linzmaier et al. 2018). However, we propose that the methods used in this study stand to highlight goldfish as a species exhibiting traits that might "pre-adapt" it to establish, spread and exert ecological impact. As well as demonstrating a voracious appetite in this study, the species is known to have a highly adaptable, generalist diet, which can lead to extensive grazing on aquatic vegetation, or preying on amphibian eggs or aquatic invertebrates (Richardson et al. 1995; Monello and Wight 2001). They are also known to be highly tolerant of anoxic conditions (Fagernes et al. 2017), saline conditions up to 6 ppt (Luz et al. 2008), temperature (Ferreira et al. 2014) and their large maximum size combined with potentially long lifespan (Froese and Pauly, 2022), may make them more likely to be released by pet owners (Duggan et al. 2006).

Going forward, we encourage further impact assessment methods that account for propagule pressure, predatory impact and dispersal-enhancing behavioural traits, and propose that the RIR methods introduced here offer a way of doing so by combining such findings. While the study species here were selected based on availability from one pet shop survey, the global pet market is taxonomically dynamic, with major shifts in species availability over time (Lockwood et al. 2019), and therefore warrants continued observation. Alternative sources of information such as listings of the species being imported into or exported from a country, e.g. the US Law Enforcement Management Information System (LEMIS) database (Fujisaki et al. 2010; García-Díaz et al. 2015), and informal online marketplaces (Olden et al. 2021) are similarly in need of monitoring. The creation of a database whereby IR scores can be generated in real time as availability changes, could provide policy makers with a valuable information source and a means to reduce the risk proactively, instead of reactively (Simberloff 2006). It could also inform law changes and help make previous "dead letters" implementable (Patoka et al. 2018).

In terms of the constituent elements of RIR, comparative functional responses using alternative native prey species might offer further insights into foraging interactions, and for "benthic grazers" like goldfish, the addition of relevant substrate and different degrees of habitat complexity (Wasserman et al. 2016; Cuthbert et al. 2019a) may add greater realism. We advocate for future assessment measures that account for dispersal enhancing traits to do so alongside different biotic and abiotic contexts relevant across different invasion stages (Smith and Blumstein 2010), and niche similarity with any potential recipient system (Liu et al. 2020; Broennimann et al. 2021) and measures of survival and reproduction (Kouba et al. 2021), could aid the prioritising of potential IAS for study. Further, behaviour studies that assess the degree of naiveté towards native predators, e.g. through chemical or visual predator cues (Lönnstedt et al. 2012; McCoy et al. 2012; Martin 2014), could help determine the degree of "pre-adaptation" of potential pet shop IAS to novel recipient ecosystems, and therefore aid management prioritisation and regulation.

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Supplementary material 1

Table S1

Authors: James W. E. Dickey, Gareth Arnott, Ciara L. O. McGlade, Andrew Moore, Gillian E. Riddell, Jaimie T. A. Dick

Data type: Csv file.

Explanation note: Temperate, freshwater species recorded during Northern Ireland pet shop survey between the 31 January and the 1 March 2017. Numbers in the Availability column refer to number of pet shops out of the twenty shops surveyed that had the listed species present. Numbers in square brackets refer to shops were the species was not observed, but there was signage to indicate the recent presence of the species. Known invasion history determined from fishbase.de, with Y indicative of at least one established non-native population.

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Link: https://doi.org/10.3897/neobiota.73.80542.suppl1

Supplementary material 2

Figure S1

Authors: James W. E. Dickey, Gareth Arnott, Ciara L. O. McGlade, Andrew Moore, Gillian E. Riddell, Jaimie T. A. Dick

Data type: Csv file.

Explanation note: Experimental set-up relating to the novel object experiment. Zone 1 covered with a metallic mesh to provide shelter for each fish, while the novel object was placed in Zone 4.

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Link: https://doi.org/10.3897/neobiota.73.80542.suppl2

Supplementary material 3

Figure S2

Authors: James W. E. Dickey, Gareth Arnott, Ciara L. O. McGlade, Andrew Moore, Gillian E. Riddell, Jaimie T. A. Dick

Data type: Csv file.

Explanation note: Novel object experimental procedure.

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